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Plant life history stage and nurse age change the development of ecological networks in an arid ecosystem

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Abstract

Understanding how ecological networks are organised over the course of an organism's lifetime is crucial for predicting the dynamics of interacting populations and communities across temporal scales. However, most studies so far considered only one life history stage at a time, such as adult, when studying networks of interacting species. Therefore, knowledge about how multiple life history stages affect the development and stability of plant–plant association networks is lacking. We measured the understory adult plant community and the soil seed bank across a plant age gradient of the nurse shrub *Retama sphaerocarpa* in an arid ecosystem in Spain. Using a multilayer network approach, we built adult understory–nurse and seed bank–nurse networks and analysed how network nestedness, species' role, and species specificity varied between them and with nurse plant age. We found that seed bank and adult understory networks changed depending on nurse plant age in two different ways. With increasing nurse plant age, adult understory networks became significantly more nested than seed bank networks. The nested architecture of seed bank networks was therefore a poor predictor of adult understory network nestedness. The contribution and specificity of species to network nestedness increased with increasing nurse plant age more in the adult understory than in seed bank networks, despite high species turnover. Our data show that life history and ontogeny affect the development of plant–plant association networks. Niche construction and environmental filtering along nurse ontogeny seem pivotal mechanisms structuring adult understory networks while the assembly of seed bank networks seems rather stochastic. We highlight the importance of mature plant communities for maintaining rare species populations and supporting the stability of ecological communities through time.

Keywords: biodiversity, ecological networks, facilitation, life history stages, multilayer networks, nurse effect, plant interaction, plant–plant networks, plant age, seed bank

Introduction

Positive interactions between plants have often been analysed by looking at the effect of nurse plants on associated species (Callaway 2007, Brooker et al. 2008, Pugnaire et al. 2011), i.e., pairwise interactions. More recently, however, attention shifted to the community level, identifying the role of nurse plants for increasing biodiversity (Butterfield et al. 2013, Cavieres et al. 2014, Kikvidze et al. 2015, Pistón et al. 2016). However, few studies have shown how interactions between nurse plants and associated species could also affect network-level biodiversity patterns (Verdù and Valiente-Banuet 2008, Saiz and Alados 2011, Losapio and Schöb 2017).

Network theory allows to analyse species interactions at the community level and the consequences of those interactions for biodiversity patterns (Bascompte et al. 2003, Vázquez et al. 2009, Tylianakis and Morris 2017). Plant–plant association networks have been described in natural plant communities across a wide range of ecosystems including tropical forests (Burns 2007), deserts (Verdù and Valiente-Banuet 2008), Mediterranean grasslands (Saiz and Alados 2011) and alpine tundras (Losapio and Schöb 2017, Losapio et al. 2017). Particularly, positive interactions among plants have been shown to make communities more resistant to extinction thanks to their nested network architecture (Verdù and Valiente-Banuet 2008, Losapio et al. 2017). Nestedness is a property of networks common to several ecological systems which is related to the degree of species aggregation where specialists interact with a small core of generalist species (Bascompte et al. 2003, Ulrich and Gotelli 2007, Almeida-Neto et al. 2008, Vázquez et al. 2009). However, most studies examining plant–plant association networks considered only one life-history stage, namely adult plants, and ignored potential changes in network nestedness with ontogeny of the nurse plant or different life history stages of the associated species.

Individuals within populations vary in life history stage (e.g., seed, germination, growth, reproduction) and ontogeny (e.g., seedling, sapling, adult). An important factor markedly changing during lifetime is the age of plants, which affects interaction intensity (Armas and Pugnaire 2005). In this way, the effects of nurse plants on understory species may vary with the age of nurses and with life-history stages of understory species (Callaway 2007, Pugnaire et al. 2011). In arid ecosystems, some legume shrubs such as *Retama sphaerocarpa* act as nurses, structuring plant communities and supporting biodiversity (Pugnaire et al. 1996, Moro et al. 1997, Pugnaire et al. 2011, Schöb et al. 2013a, O'Brien et al. 2017). On the one hand, the positive effects of *Retama sphaerocarpa* on the understory community increase with increasing age of nurse plants (Pugnaire et al. 1996, Moro et al. 1997), although the ontogeny of nurse plants represents also an ecological succession (Pugnaire et al. 2006). On the other hand, the response of understory species to nurse ontogeny varies in such a way that the soil seed bank is rather uniform while adult plants occur selectively (Pugnaire and Lázaro 2000, Callaway 2007). Nevertheless, knowledge about the response of association networks between nurses and the understory plant community as affected by plant life history is lacking. Incorporating life history and ontogeny into network theory would, thus, provide a valuable mechanistic approach for understanding processes shaping ecological networks and for predicting the dynamics of populations and communities (Cohen et al. 2003, Woodward et al. 2005, Tylianakis and Morris 2017).

Here, we examined how two plant life history stages (seeds and adult plants) of understory species and nurse plant ontogeny (i.e., age) influence network architecture in an arid environment. Particularly, we assessed (i) how the nested architecture of adult understory–nurse and understory seed bank–nurse networks vary with nurse age, which would point towards a potential role of the nurse ontogeny working like an environmental filter; (ii) whether the nested architecture of seed bank networks predicts that of adult understory

networks, which would point towards a potential role of dispersal limitation or recruitment for plant community assembly; and (iii) how the role and specificity of species within networks vary with life history stage and nurse age, which would point towards the contribution of ontogeny and life history for species persistence. We hypothesised that different plant life history stages and ontogenetic stages contribute to the structuring of plant–plant association networks. We expected that nurse ontogeny affected the roles of species within the nested architecture of networks.

Material and methods

Study area and nurse plant

We reanalysed data from a previously published study (Pugnaire and Lázaro 2000) performed in the arid environment of the Tabernas desert (Spain, 37°08' N, 2°22' W, 630 m elevation).

The climate of this area is arid, with mean annual temperature of 16°C and 256 mm of mean annual precipitation (Pugnaire and Lázaro 2000). Here, the nurse, the legume shrub *Retama sphaerocarpa* (L.) Boiss. (Fabaceae, hereafter *Retama*), creates ‘fertility islands’ beneath its canopy by increasing soil organic matter, soil water content and generally ameliorating the growing conditions for understory plants. Therefore, *Retama* plays a critical role for community structure and biodiversity (Pugnaire et al. 1996, Moro et al. 1997, Pugnaire and Lázaro 2000, Pugnaire et al. 2006, Armas et al. 2011, Pugnaire et al. 2011, Schöb et al. 2013a, O’Brien et al. 2017). The study site was a relatively homogenous area of c. 2 ha, with a patchy plant community dominated by *Retama*. Fifty shrubs were randomly selected in a mixed population on the floodplain of the valley. We used nurse shrub age from Pugnaire et al. (1996), which was estimated by the diameter of the thickest branch. Then, shrubs were sorted in order of increasing age and grouped into five balanced age-classes in order to build five nurse networks, each composed by ten nurse replicates (Supplementary material Appendix 1, Table A1). The composition of the understory plant community was determined

beneath each individual *Retama* shrub (Pugnaire et al. 1996; summary data in Supplementary material Appendix 1, Tab. A2). To measure soil seed bank, the upper 3 cm layer was sampled at an intermediate point between the canopy edge and the centre, and bulked from four thoroughly mixed subsamples (one by each of four aspects except for very small shrubs) which represented *c.* 250 cm² of soil surface per shrub. Polyethylene pots were filled with a mixture of vermiculite and perlite in a 1:1 proportion on top of which was placed a volume of natural soil from each of the 50 samples equivalent to 150 ml of dry soil. Seed bank was sampled in September when the seed bank is bigger and species emergence as seedlings from seeds, including annual and perennial species, was recorded after seven months (Pugnaire and Lázaro 2000; summary data in Supplementary material Appendix 1, Tab. A3).

Network analysis

The overall plant multilayer network was represented by three interconnected layers: the nurse, the adult understory and the understory seed bank (Figure 1). For each age class *a* (*n*=5), we built adult understory–nurse networks G_{us} and seed bank–nurse networks G_{sb} as bipartite undirected networks $G = (U, V, E)$, where *U* and *V* represented adult or seed bank plant species u_i and nurse plants v_j , respectively, and *E* the presence–absence links indicating the co-occurrence $e_{u,v}$ between an adult or seed bank species u_i and an individual nurse plant v_j . We created five networks per life history stage each containing 10 nurse plants and a variable number of adult understory and seed bank species, comprising overall 106 and 86 plant species, respectively (Supplementary material Appendix 1, Tab. A1, A2). A co-occurrence link $e_{u,v}$ was drawn in the network G_{us} or G_{sb} if a plant species u_i was present in the understory of a nurse plant v_j as an adult or in the seed bank, respectively.

We first quantified the nested architecture of bipartite networks across the nurse age gradient. We used the nestedness measure of NODF (Almeida-Neto et al. 2008) to summarise

how different adult and seed bank species were distributed among nurse age classes. NODF is based on paired overlap (i.e., the percentage of identical co-occurrence patterns) and decreasing fill (i.e., differences in the sum of co-occurrence links between any pair of plant species and nurse plants) of the network matrix. Large NODF values indicate nesting, such that the distribution of rare species is a subset of plots with common species, while small values indicate clustering and turnover. Nestedness may arise from differential rates of colonisation and extinction of plants beneath nurses. Anti-nested patterns may result from replacement of similar species across environmental gradients (Ulrich and Gotelli 2007, Vázquez et al. 2009, Tylianakis and Morris 2017)

To compare the nestedness values between networks across the age gradient, we controlled for differences in matrix size (U , V) by using a null model approach (Ulrich and Gotelli 2007, Ulrich et al. 2009). We estimated the deviance z between the observed nestedness and the random expectation given by the probabilistic null model (Bascompte et al. 2003). The probabilistic null model builds networks from a template of probabilities, such that in a network G the probability of drawing a link $e_{u,v}$ between a plant species u_i and a nurse plant v_j is $p_{u,v} = \frac{1}{2}(\frac{n_u}{U} + \frac{n_v}{V})$, where n is the number of links of species u_i and nurse v_j weighted by the number of plant species U and nurse plants V , respectively (Bascompte et al. 2003). For each layer across the gradient we built 100 replicates of the probabilistic null model keeping the matrix size of probabilistic networks equals to the respective observed network. This null model performs better in reproducing the interaction patterns and in balancing type I and type II errors. We calculated $z = \frac{o-r}{sd(r)}$, where o and r are the NODF values of observed and probabilistic networks, respectively, weighted by the standard deviation sd of probabilistic network NODFs. This z -NODF represents the unit of network replication for further statistical analysis ($n= 100$ z -NODFs per nurse age per life history stage; sample size = 1000).

Second, we quantified each plant species' role and response to the assembly of networks across the age gradient. We used the individual nestedness contribution of species c (Saavedra et al. 2011) to summarise the role of each plant species in supporting the network. We calculated this nestedness contribution c for each plant species U in each of the observed networks as the degree to which the observed network nestedness compares to the value obtained when randomising just the interactions of that particular species (Saavedra et al. 2011). The higher the contribution of a species to nestedness, the greater the overall contribution to network persistence. Then, to assess the distribution of species between networks across the gradient, we calculated the species specificity index SSI (Julliard et al. 2006) of plant species. We calculated this index for each plant species U in each observed network G_{us} and G_{sb} as the variance of the coefficient of variation of plant–nurse links (Julliard et al. 2006). Low values suggest high generality while high values suggest high specificity.

Statistical analysis

To test the variation in network nestedness across the nurse age gradient, we used a regression model with z -NODF as response and nurse age (ordered factor), life history stage and their interaction as predictors. To test whether nestedness of seed bank–nurse networks predicts nestedness of adult understory–nurse networks we used a regression model with the adult understory z -NODF as response and nurse age (ordered factor), seed bank z -NODF and their interaction as predictors. We used relative nestedness z -NODF as response variable instead of observed NODF values in order to compare among networks (for observed NODF values see Supplementary material Figure A1). This approach was necessary to account for differences in matrix size and shape when comparing across different networks (Ulrich and Gotelli 2007, Ulrich et al. 2009). To test the variation in the contribution of plant species to

network structure and specificity of plant species distribution, we used linear mixed-effects models with nestedness contribution c and species specificity SSI of each species u_i as response (two separate models) and nurse age (ordered factor), understory life history stage and their interaction as fixed effects, and species identity as random effect. To account for the increasing sampling area beneath shrubs with increasing nurse age, canopy area was included as covariate and fitted as first predictor in all models. In this way, eventual significance of the predictor ‘nurse age’ would indicate effects beyond simple sampling area effects. For each model, the significance of predictors was tested via chi-square test in terms of explained variance. Network and statistical analyses were performed in R version 3.3.3 (R Core Team 2017), using the *bipartite* package (Dormann et al. 2008) for network analysis and the *nlme* package for mixed-effects models (Pinheiro et al. 2016).

Results

Network nested architecture

After accounting for nurse canopy area ($F_{1,989} = 150.95$, $p < 0.0001$), nestedness significantly differed between adult–nurse and seed bank–nurse networks across the nurse age gradient ($F_{4,989} = 49.28$, $p < 0.0001$, $R^2 = 0.732$, Figure 2, Table 1). This indicates differential effects of nurse age on the two network nested architectures. Specifically, the marginal average (i.e., the mean of responses independently from each other) of adult–nurse network nestedness changed about two and a half times more than that of seed bank–nurse network nestedness ($\hat{\beta}_{us} = 3.93$, 95% CI = 3.86–4.01 and $\hat{\beta}_{sb} = 1.61$, 95% CI = 1.53–1.69, respectively).

After controlling for the effects of canopy area and nurse plant age ($F_{1,489} = 182.10$, $p < 0.0001$ and $F_{4,489} = 215.05$, $p < 0.0001$, respectively), nestedness of seed bank–nurse networks was a poor predictor of the nestedness of adult–nurse networks, neither as a main effect nor in interaction with nurse age ($F_{1,489} = 0.23$, $p = 0.6341$ and $F_{4,489} = 0.31$, $p = 0.8739$,

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respectively; $R^2 = 0.674$, Figure 3, Table 1). This indicates the contribution of life history stage and nurse age to network nested architecture and the lack of potential causal relationships between the two networks.

Species functional roles

After accounting for nurse canopy area ($F_{1,479} = 0.84$, $p = 0.3590$), the contribution of species to nestedness varied with nurse age ($F_{4,479} = 3.28$, $p = 0.0114$) and in two different ways between adult–nurse and seed bank–nurse networks ($F_{4,479} = 8.62$, $p = 0.0035$) across the nurse age gradient (interaction term: $F_{1,479} = 2.82$, $p = 0.0248$, $R^2 = 0.617$, Figure 4A, Table 1). In particular, nested contribution tended to increase more in adult understory–nurse networks than in seed bank–nurse networks (Figure 4A), changing from negative to positive with increasing nurse age.

Similarly, the specificity of species varied with nurse age ($F_{4,479} = 2.63$, $p = 0.0336$) and was marginally significantly different between adult–nurse and seed bank–nurse networks depending on nurse age (interaction term: $F_{4,479} = 2.16$, $p = 0.0727$, $R^2 = 0.519$, Figure 4B, Table 1). In particular, species specificity showed an increasing trend in adult understory–nurse networks while it remained constant in seed bank–nurse networks (Figure 4B).

Discussion

Our hypothesis that life history and ontogeny affect the development of plant–plant association networks was supported by our data. We found that seed bank and adult understory networks changed depending on nurse plant age in two different ways. The nested architecture of adult understory networks increased with increasing nurse age while seed bank networks varied independently of nurse age. Contrary to our expectations, seed bank network architecture was a poor predictor of adult understory network architecture. These results

indicate that differences in nestedness of adult understory networks among different nurse age classes were independent from seed bank networks. Finally, the contribution and specificity of species to network nested architecture increased with increasing nurse age more in adult understory than in the seed bank. Taken together, these data suggest that different ecological processes may drive the species composition depending on life history stage. We can conclude that nurse age structures adult plant networks modifying niche space and acting as environmental filter, while the assembly of the seed bank seems rather stochastic.

The variability in species composition and their interactions along environmental gradients may arise in organised interaction networks with a nested architecture (Ulrich and Gotelli 2007, Tylianakis and Morris 2017). In particular, an increasingly nested distribution may arise from a differential rate of colonisation and extinction of understory plants (Ulrich and Gotelli 2007, Vázquez et al. 2009, Tylianakis and Morris 2017). Consistent with theory (Grime 1973), we found that the rate of understory species turnover increased across the nurse age gradient up to the third nurse-age class, with more adult plant species colonising the understory with increasing age compared to the number of species that disappeared (Supplementary material Appendix 1, Fig. A2A). The increase in nestedness in adult understory–nurse networks indicates that adult plant species occurring beneath small nurse plants represent a subset of the most common species that also occur beneath large nurse plants. This implies that, during the ontogeny of the nurse, rare species successively enter the local understory community. On the other hand, despite a high species turnover, the rates of species colonisation and disappearance in the seed bank balanced each other across the gradient (Supplementary material Appendix 1, Fig. A2B).

These results suggest that nurse plant age and life history stages mediate the nested architecture of plant–plant association networks. Positive effects of nurse plants on soil fertility increase with age and size as nutrient content and water availability is higher beneath

older and bigger compared to younger and smaller shrubs (Pugnaire et al., 1996, 2011, Mihoč et al. 2016). These changes in microhabitat conditions with ontogeny affect the composition and increase the diversity of the understory plant community (Pugnaire et al., 2006, O'Brien et al. 2017), while they have no consequences on the seed bank (Pugnaire and Lazaro 2000). As nurse size is linked to nurse age and successional dynamics (Pugnaire et al. 2006), these results imply that also time affects the development of plant–plant networks. The older the shrub, the longer the time the shrub acted as a nurse, the more the time is available for successional dynamics to enable understory species interacting with nurse plants. Moreover, the nestedness of seed bank networks was not important for predicting the nested architecture of adult understory networks. This indicates that seed bank–nurse interactions poorly affect networks of the adult understory and nurse plants. Potential underlying mechanisms may be different rates of survival and mortality among understory species across nurse plants differing in age, while the limitation to dispersal and colonization (i.e., the failure of seeds to disperse homogeneously over the habitat) may be less important. Taken together, these results suggest that the nested architecture of adult understory–nurse networks is most likely driven by nurse-mediated microhabitat modification (Schöb et al. 2012). Indeed, the less stressful environment under older and bigger shrubs could result in larger niche space beneath them (Schöb et al. 2013b). Any increase of niche space and niche differentiation that sufficiently reduces interspecific competition (Chesson 2000) may thus increase the nestedness and stability of ecological networks (Bastolla et al. 2009). An alternative and complementary mechanism may be that the increase of nurse age and size underpins morphological differences between nurse plants and understory species. These morphological differences may support higher asymmetry in the interactions between nurses and understory species, which may, in turn, increase nestedness (Bascompte et al. 2003, Vázquez et al. 2009).

In the adult understory, the contribution of species to network nested architecture increased with increasing nurse age, which is consistent with the observed increase in overall adult understory network nestedness. This indicates that species that most strongly increased network stability were more common in association with older nurse plants. In accordance with theoretical predictions (Saavedra et al. 2011), those species contributing the most to nestedness are also rare species that occur only beneath big and old nurse plants. In other words, the persistence of understory–nurse networks is supported by big and old nurse plants hosting rare plant species, which highlights the importance of old individuals for maintaining biodiversity and supporting the stability of ecological networks. Contrary to previous knowledge about the constancy of species’ role across gradients (Tylianakis and Morris 2017), our findings highlight that species’ role in networks could vary, even within the same ecosystem, depending on ontogeny. Similarly, the contribution of adult understory species to network nested architecture became increasingly species-specific with increasing nurse plant age. This indicates that species tended to specialise and segregate across the ontogenetic gradient (see also Julliard et al. 2006). It also suggests an expansion of niche space associated with nurse-mediated microhabitat modification, in agreement with previous reports from other nurse plant systems (Schöb et al., 2012, 2013b). Conversely, in seed bank–nurse networks the contribution of species to nestedness varied less than in understory–nurse networks and the species specificity was constant across the nurse age gradient. These results indicate that, in contrast to adult understory networks, species’ roles and the overall level of specificity remained more stable in seed bank networks, in line with the expectation of species’ role constancy (Tylianakis and Morris 2017). This was surprising given the 50% species turnover in the seed bank community (Supplementary material Appendix 1, Fig. A2B). Consequently, there was a replacement of species with no modification of their functional and structural roles within the network (i.e., contribution and specificity). This

indicates that the organisation of species interactions within seed bank networks remains stable despite changes in community composition.

Variability in the architecture of ecological networks has found to be substantial between life histories and across ontogeny which is consistent with general patterns described across spatial and temporal gradients (Tylianakis and Morris 2017). Interestingly, our study suggests that network architecture changes with the characteristics of organisms during their lifetime, an observation also made in marine food webs where the network architecture shifts during ontogeny of predators and prey (Leeuwen et al. 2014). The contrasting responses of adult understory and seed bank networks suggest that both deterministic and stochastic processes are operating. Habitat modification and niche construction by nurse plants can drive the development of nested architecture and the role of species in adult understory–nurse networks. However, within the seed bank, roles and responses may be more similar among species making therefore facilitation processes less important and maintaining homogeneous networks regardless of species composition and turnover. The focus on facilitation networks when studying habitat modification by nurse plants is expanding our understanding of species interactions at the community level beyond pairwise competition. Further consideration of life histories traits and ontogeny of interacting species can advance our understanding of the forces shaping ecological networks through time.

Declarations

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Figure legends

Figure 1. Overview of the plant multilayer network represented by the seed bank (left), the nurse plants with different age (middle) and the adult understory plant community (right).

A network composed of ten nurse plants was built for each nurse age class (five age classes in total, here depicted three for simplicity).

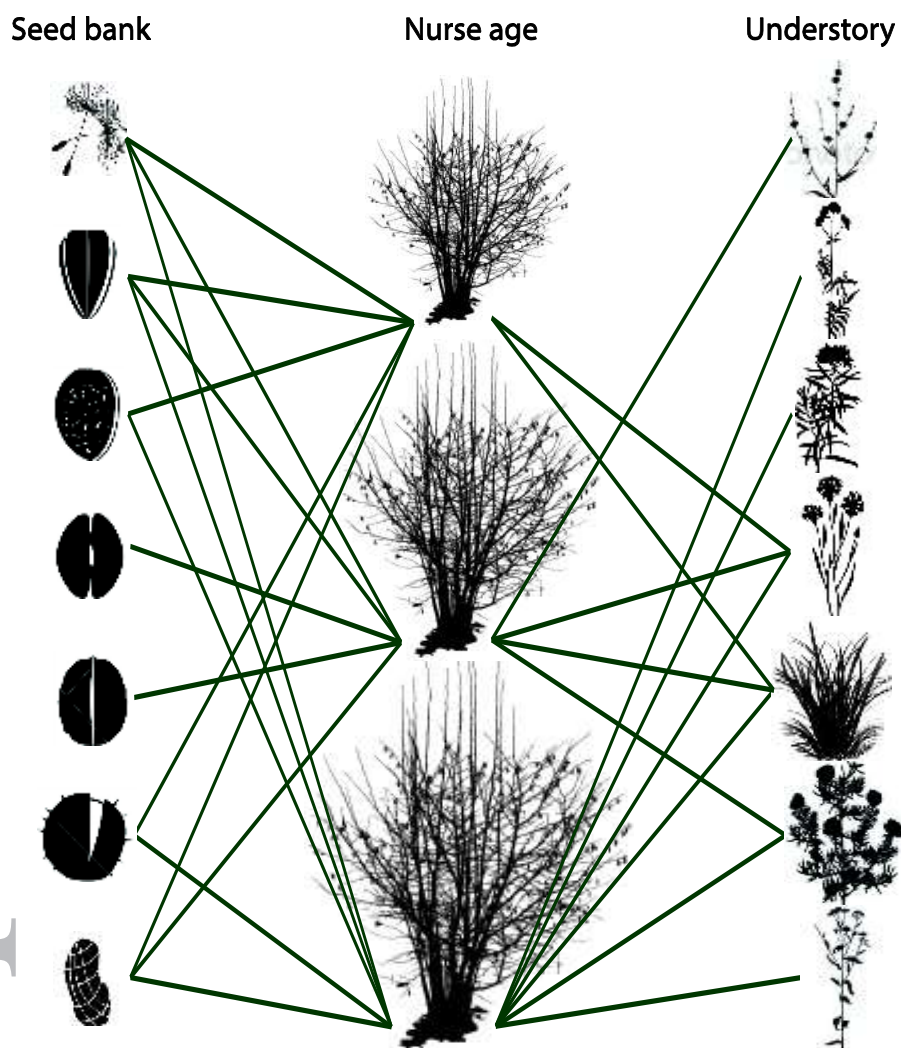


Figure 2. Network nested architecture across the gradient of nurse age. Each dot represents the relative nestedness, measured with NODF and calculated as the difference between observed and probabilistic networks, in (A) adult understory–nurse networks and (B) seed-bank–nurse networks. Predicted marginal means and 95% CI shown.

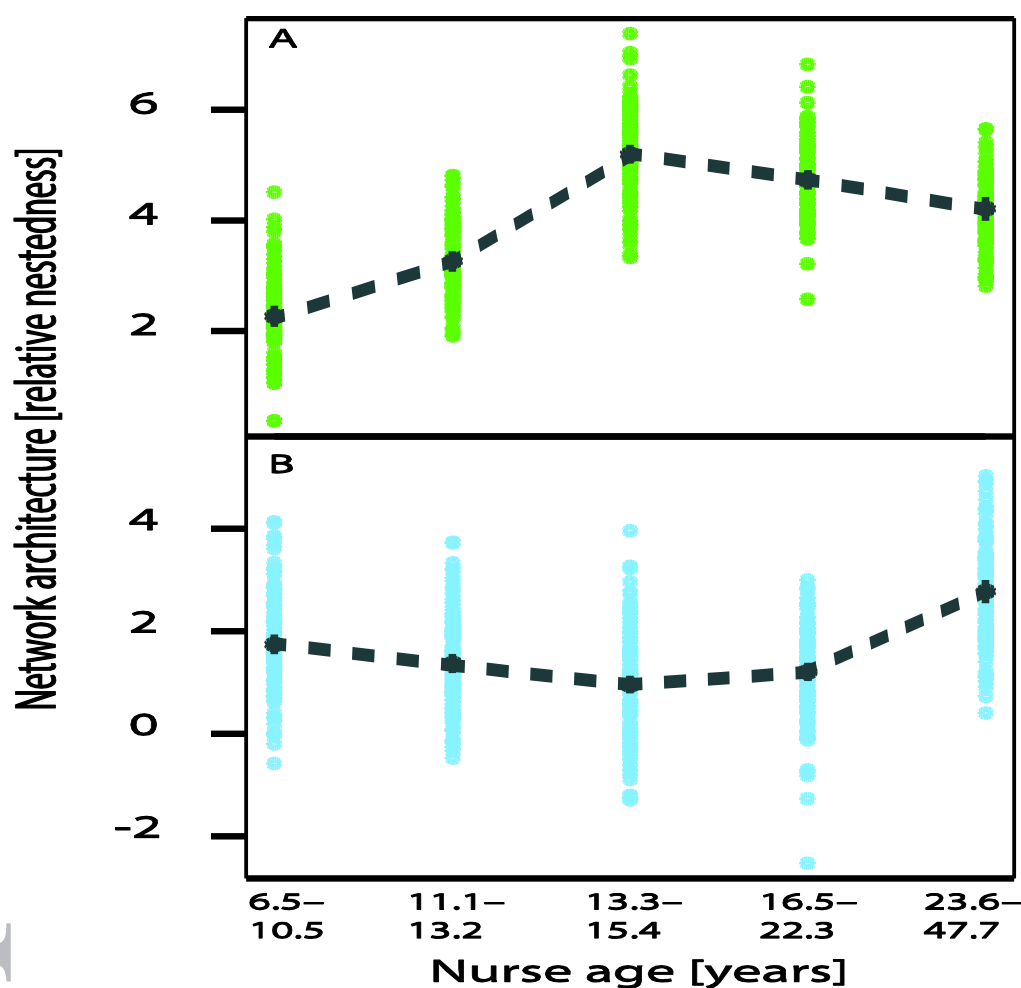


Figure 3. The effects of nested architecture of seed bank–nurse networks on adult understory–nurse networks (x-axis, regression coefficient and CI) across the nurse age gradient (y-axis). Each dot represents the predicted mean effect (95% CI) of seed bank network nestedness on understory network nestedness for each nurse age class.

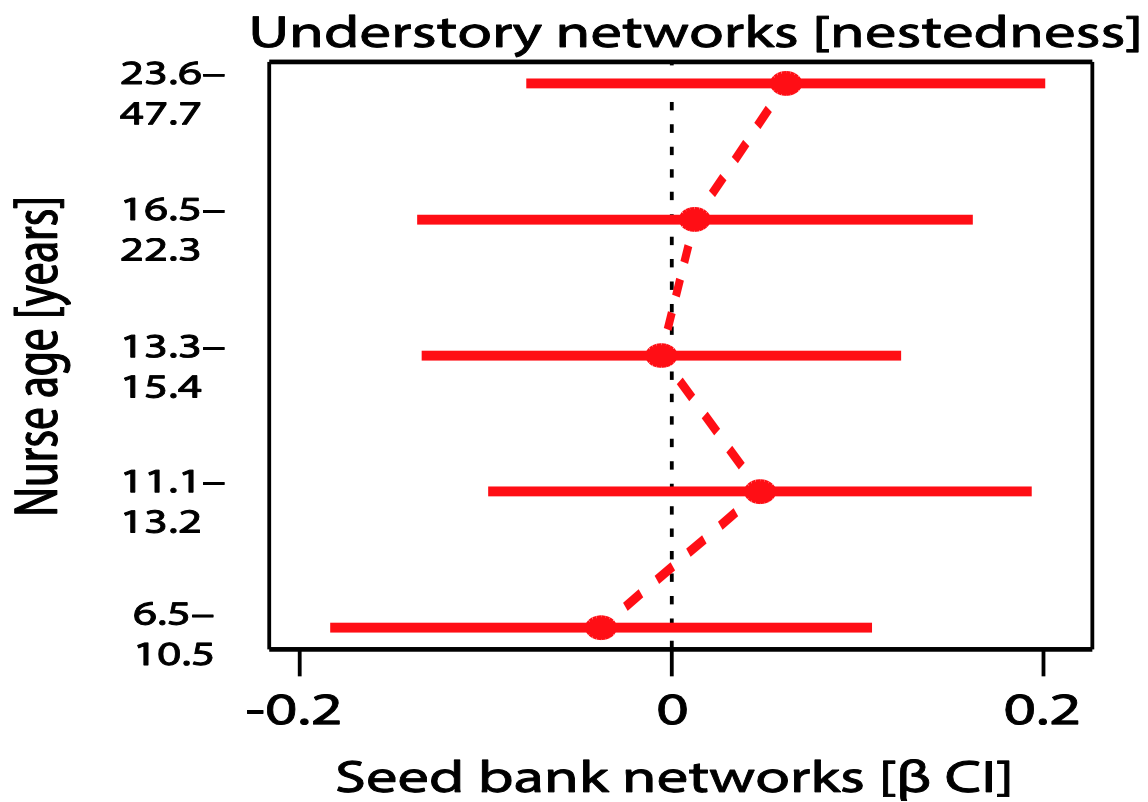


Figure 4. Functional role and species response across the nurse age gradient. Dots represent the predicted marginal means (95% CI) of adult understory–nurse networks (green) and seed bank–nurse networks (blue) across the nurse age gradient. (A) Contribution of species to nestedness and (B) specificity of each plant species.

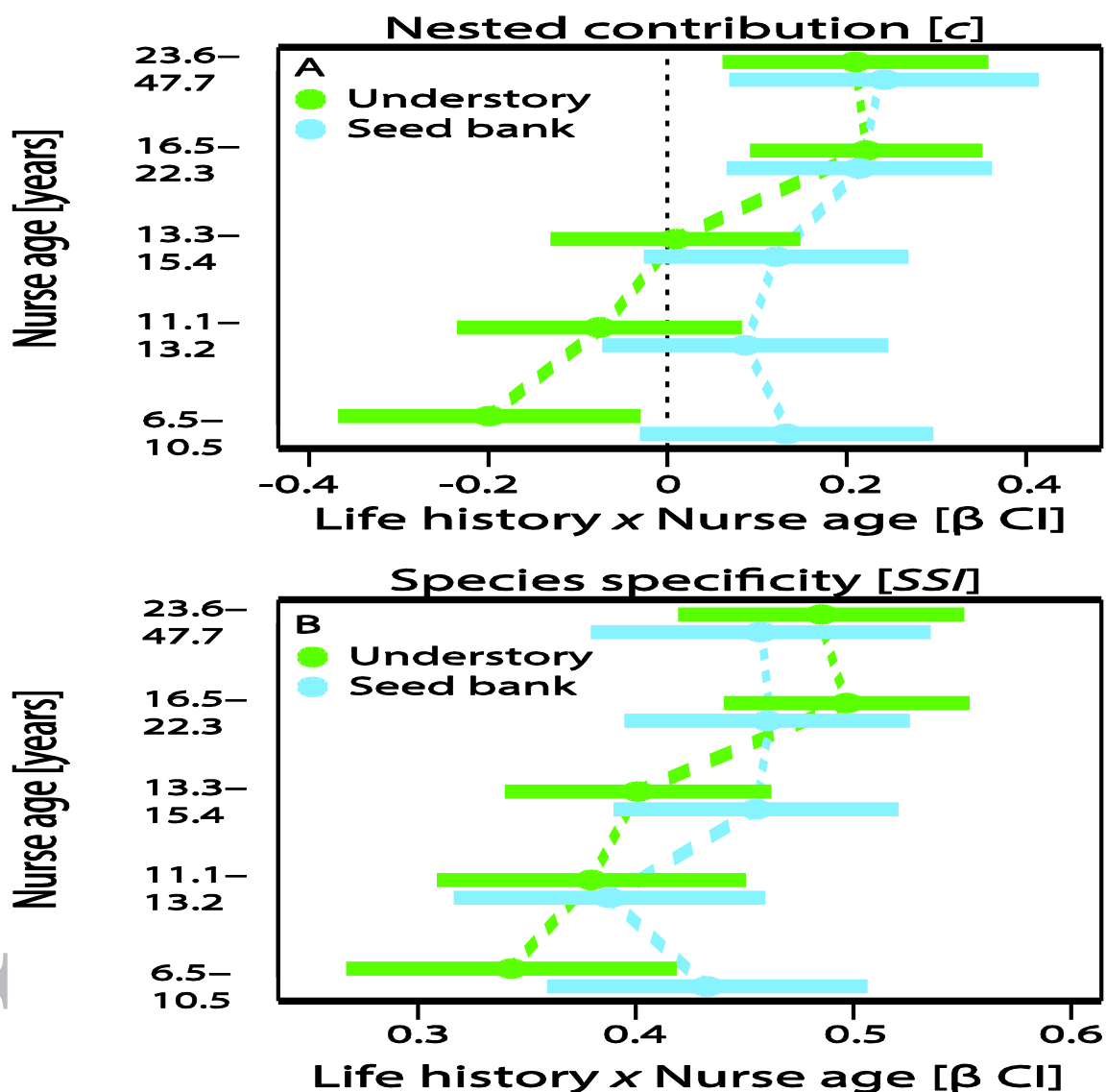


Table Legend

Table 1 Summary of regression models to analyse changes in the nested architecture of networks (nestedness = area + nurse age x life history) and adult understory nestedness as a function of seed bank nestedness (understory = area + nurse age x seed bank). Linear mixed-effects models were used to analyse changes in species functional role (N contribution = $X(\text{area} + \text{nurse age} \times \text{life history}) + Z(\text{species identity})$) and species specificity (specificity = $X(\text{area} + \text{nurse age} \times \text{life history}) + Z(\text{species identity})$), where X and Z indicate fixed and random effects, respectively. Overall, the species pool of adult understory and seed bank communities consist of 106 and 86 species, respectively.

Response	Predictor	F	Df	<i>p</i>
Nestedness	Area	150.95	1,989	< 0.0001
	Nurse age	49.28	4,989	< 0.0001
	Life history	1774.02	1,989	< 0.0001
	Age:Life h	154.23	4,989	< 0.0001
Understory	Area	182.10	1,489	< 0.0001
	Nurse age	215.05	4,489	< 0.0001
	Seed bank	0.23	1,489	0.6341
	Age:Seed bank	0.31	4,489	0.8739
N contribution	Area	0.84	1,479	0.3590
	Nurse age	3.28	4,479	0.0114
	Life history	8.62	1,479	0.0035
	Age:Life h	2.82	4,479	0.0248
Specificity	Area	1.58	1,479	0.2087
	Nurse age	2.63	4,479	0.0336
	Life history	0.42	1,479	0.5180

